Influence of Past Interactions on the Prairie Today: A Hypothesis

Kathleen Keeler
University of Nebraska - Lincoln, kkeeler1@unl.edu

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INFLUENCE OF PAST INTERACTIONS ON THE PRAIRIE TODAY: A HYPOTHESIS

Kathleen H. Keeler

School of Biological Sciences
University of Nebraska-Lincoln
Lincoln NE 68588-0118
kkeeler1@unl.edu

ABSTRACT—Past conditions in North American prairies have left behind animals and plants whose features were shaped by interactions, some of which no longer exist. For example, pronghorns are fast runners but there are now no fast predators to chase them. Similarly, bison activity structured grasslands, but few prairie reserves now have bison. Here I draw attention to possible cases where ecological patterns are best explained by conditions not present in the modern prairie and propose that such outcomes may be more important than presently thought. My aim is to stimulate a reevaluation of prairie organisms and the effect of their interactions in light of this hypothesis.

The debris covered ten thousand years and it wasn't much, considering the time, nor was it easy to measure the intervals from one chipped stone to another. . . . (L. Eiseley, "The High Plains" in *Notes of an Alchemist* 1972)

Introduction

Everyone appreciates that the past plays a role in determining the present, but in the Great Plains we are often ignorant of the biological aspects of our history. Organisms and interactions now absent have influenced the organisms and interactions we see today.

No history of the Great Plains would fail to mention the great sweep of Pleistocene glaciations south across North America, and the extinction of large animals that occurred at roughly the same time (e.g., Kurtén and Anderson 1980; Martin and Klein 1984). Also, the arrival of the horse (*Equus equus*) from Europe is part of our traditional understanding. The horse transformed the lives of the Plains tribes and the relationships between them (e.g., White 1978; Sherow 1992). Contact with Europe and expansion of the United States brought more changes, exemplified by the near-extinction of bison (*Bison bison*), plowing of most of the tallgrass prairie, and the establishment of major urban areas in the region (Samson and Knopf 1996; Licht 1997). I suggest that we have not yet noted all the consequences of these major historical events.

Past Organisms

Extinctions

Species extinctions always leave a biological gap. The missing organisms competed for (resources space or water), ate something, and were eaten by others. All such relationships cease with extinction. However, the traits or behavior patterns that were part of the interaction are likely to persist for a long time. For example in 1973 on the Island of Mauritius, the tree *Calvaria major* existed as a total population of 13 trees, all of them huge and probably 300 years old. The trees flowered and produced seeds, but the seeds never sprouted. Temple (1977) showed that the seedlings inside the seeds were healthy but unable to break out of the very hard seed coat. Filing the seeds or force-feeding them to turkeys allowed the seeds to germinate, and there are now many young trees. He argued that the seed coat had evolved to protect the seeds when they were eaten by dodo birds (*Raphus cucullatus*). However, dodo birds went extinct about 1680 (Day 1981), so the tree was going extinct for lack of successful seedlings related to the missing interaction of the dodo bird. How many similar situations have been created by extinctions in the Great Plains?

During the Pleistocene, the last one to two million years, some 200 genera of mammals greater than 44 kg (100 pounds, a large dog) went extinct (Martin 1967; 1973). Between the major glacial advances of this epoch, central North America was home to a much more diverse fauna than the prairies of 200 years ago. Camels, horses, ground sloths, mammoths, mastodons, sabertooth cats . . . the list of extinct mammals is long and relatively well-known (Martin 1967; Kurtén and Anderson 1980; Pielou 1991).

There are many unsolved issues associated with these Pleistocene extinctions. Prehistoric interactions of which we are unaware undoubtedly influenced familiar native animals. One likely example is the pronghorn (*Antilocapra americana*). For sustained speed, the pronghorn is the fastest animal in the Western Hemisphere, and maybe in the world. It is capable of maintaining 56 km/hr (35 mi/hr) for more than 11 km (7 mi) (Costello 1969;

Yoakum 1978), and its maximum speed appears to be in excess of 96 km/hr (60 mi/hr) (Van Wormer 1969). There is no North American predator today whose attacks require such great escape speed. The swiftest living predator, the prairie wolf (*Canis lupus*), uses a relay system that involves chasing its prey in a circle; this allows a second wolf to cut across the circle rather than following the prey. Against the pronghorn's straight-line run, this strategy is useless (Costello 1969). The faster carnivores from which the pronghorn likely ran can no longer be found.

Another possible consequence of the Pleistocene extinction is that the loss of the big Pleistocene herbivores left some plants without dispersers. Janzen and Martin (1982) argued that in the American tropics at least 37 species appear to have fruits designed to be eaten and the seeds dispersed by big animals that are now extinct. While it is logical that the extinction of big animals changed interactions in the ecosystem, evidence of specific effects is difficult to obtain or test (see critique by Howe 1985). If Pleistocene extinctions changed interactions in the Neotropics, it is likely that they also changed interactions in the Great Plains.

One plant in the plains with seemingly anomalous large fruits is Osage orange (*Maclura pomifera* [Raf.] Schneid.). Ecologically, Osage orange is an invader of grasslands rather than a tree of mature forests, and some portions of its native distribution "were prairie, particularly those [prairies] south of the Red River" (Smith and Perino 1981:29). The fruits are 8-12 cm in diameter (Fig. 1), average 450 gm, and have a strong, distinctive odor (Smith and Perino 1981; Barker 1987). Despite their size and potential nutritional value, no big herbivore today is known to eat them. In fact, for the most part the fruits go uneaten, although squirrels occasionally devour the seeds and woodrats cache them (Martin et al. 1961; Horne et al. 1998). It seems reasonable to suggest that some now-extinct animal with large jaws consumed the fruit, dispersing the hard seeds in its droppings. Although Osage orange is a tree and not strictly a grassland species, it is a North American endemic whose range before the coming of Europeans was apparently limited: eastern Texas and Oklahoma, plus perhaps southeastern Kansas, southwestern Missouri, Arkansas and northwestern Louisiana (Smith and Perino 1981). It has been successfully planted as far north as Colorado and southeastern Canada however (Smith and Perino 1981; Barker 1987). A restricted range is one expected consequence of the loss of wide-ranging dispersers (Janzen and Martin 1982), even though some successful dispersal must occur without the big herbivores. If not, plants requiring extinct herbivores as dispersers would have gone extinct long ago (Howe 1985). There

Figure 1. Osage orange, *Maclura pomifera*. Fruit diameter 10 cm. It looks like a fruit some big animal would eat, but none do. Photograph by R.B. Kaul.

are alternate explanations of narrow ranges, lack of fire tolerance being an obvious one for a grassland tree. But I know of no explanation of the function of Osage orange's orange-sized fruits, which is why I raise the question of extinct large dispersers.

Most grassland plants are generally of short stature, and their fruits are likewise small and easily handled by the small modern animals. Detection of the role that the missing big animals played in dispersing of their seeds is particularly difficult, since animals of many sizes can disperse small fruits. It is easy to conclude that the dispersal patterns of today have existed throughout their history. Yet, most of the plant genera are native to this region and older than the Pleistocene, so they interacted with the extinct Pleistocene animals here. Did they adapt to dispersal by those animals? We assume they did. Possible examples include sand cherries (*Prunus pumila* L. var. *besseyi* (Bailey) Gl.) or cacti (e.g., *Opuntia macrorhiza* Engelm.). Both have edible fleshy fruits, and they contain seeds that resist crushing or digestion. We know what disperses them now, fruit eaters from deer to mice to tortoises (e.g., Russell and Felker 1987). However, perhaps that is not the whole story. Perhaps some characteristics of prairie plants, such as the bright colors of cactus fruits, attracted now-extinct herbivores who dispersed them in patterns quite different from those at present.

Once species are extinct, only circumstantial arguments can be made about their impact; we will never really know. However, some species are not extinct, but simply absent from much of their historical range. More can be done to understand their impacts.

Keystone Interactions

A keystone species is one whose activities have a critical effect on community structure, whether they are numerous or not (Paine 1969). Several species have been suggested as keystone species on the Great Plains: bison (*Bison bison*), the black-tailed prairie dog (*Cynomys ludovicianus*) and beaver (*Castor canadensis*). All three of these species were greatly reduced in number over the last two centuries, and their impact lost from many areas.

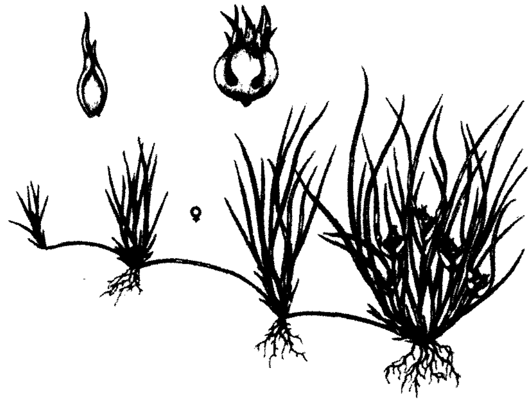
Bison. Knapp et al. (1999) argue that bison were keystone species in tallgrass prairie. They point out that bison grazing activities affect the prairie in at least four major ways: First, bison change plant species composition by selective grazing. Second, they alter the prairie physically. Their trampling causes significant compaction of the soil, and their dust wallowing creates small soil depressions (buffalo wallows) which subsequently have a distinctive plant community. Third, bison change the prairie chemical environment, by shifting nutrient cycles in a variety of ways, not the least by depositing nutrients in the form of urine and feces. And, fourth, bison increase spatial and temporal heterogeneity of the grassland. Because they do not eat or travel uniformly across the prairie, the first three effects are not distributed equally. In sum, bison alter prairies at many scales: the individual plant scale, vegetation patch scale, and the landscape scale. This kind of impact by a single species is what is expected of a keystone species. The importance of bison and their effects strongly raises the question of what interactions have been changed dramatically in the prairie remnants without bison.

While some research areas have reintroduced bison, nowhere do they occur or roam on their historic scale. Thus, we are probably ignorant of past bison-plant relationships. For example, Christy (1887) observed that the distribution of buffalo bean, now called ground-plum, (*Astragalus* *[corynocarpus]*, *crassicarpus* Nutt.) agreed fairly well with the former range of bison. Buffalo bean is very attractive to cattle, and it was probably equally so to bison, making bison potential dispersal agents.

Janzen (1984) suggested that where the most common animals are big grazers, a plant's foliage may function, like fruit, to attract herbivores who eat the whole plant and then disperse the seeds. Collins and Uno (1985) thought that this was unlikely for three reasons. First, most grasses have seeds that occur higher than does their foliage. Second, it is not clear that herbivory, from which dispersal provides an escape, is important in grasslands. And, third, where big mammals are present, e.g., in the Wichita Mountains Wildlife Refuge in Oklahoma, seeds were not seen germinating frequently out of dung along animal pathways, as would be expected from the Janzen model. Quinn et al. (1994), however, offered a specific example of foliage-as-fruit. Buffalo grass (*Buchlöe dactyloides* [Nutt.] Engelm.) is dispersed because grazers (bison) eat the plant, seeds and all. The fruits of buffalo grass are produced low on the plant, below the tops of the leaves (Fig. 2A). And, the leaves of buffalo grass are nutritious, whether fresh, or dry, or frozen under the snow. These are two characteristics needed for grazers to disperse seeds as a result of eating the plant. Finally, buffalo grass seeds germinate very well from manure, completing the Janzen model (Quinn et al. 1994). The contrast between buffalo grass and seed of the many other grasses of the high plains is striking. The seeds of most other plants mature well above the leaves, in the tallgrasses as much as a meter above (Fig. 2B; photographs in Weaver 1954).

Seeds of the dominant tallgrasses are generally thought to be distributed by gravity (e.g., McKone et al. 1998). However, considering tallgrasses in the context of animal dispersal and missing species is interesting. Big bluestem, *Andropogon gerardii* Vitman, was the dominant grass of intact tallgrass prairie. The name *Andropogon* means "bearded seed" in Latin. The seeds (actually, the single-seeded fruits) have a covering of curly hairs. The ripe seeds are at the ends of stalks 1-3 m in the air (Fig. 2B). Both hairiness and position would have assisted some seeds in attaching to bison fur. They freely attach to the hair and wool shirts of passing biologists. A single buffalo pelt carried dozens of different plant seeds (Berthoud 1892; Christy 1887; Ridley 1930). Once on the bison, they might have been carried to whereever the bison's coat was shed in the spring. Bison frequently shed their fur, with its imbedded seeds, after wandering hundreds of kilometers (Roe 1951). Thus, one consequence of bison dispersal is a huge possible range for the seeds of one plant. This would produce a very different

A



B

Figure 2. (A) The seeds of buffalo grass (*Buchloe dactyloides*) are hidden below the foliage, where they can be dispersed by being eaten by grazers, and (B) the seeds of big bluestem (*Andropogon gerardii*) are positioned 2 m off the ground, where they can be dispersed on the fur of buffalo. Reproduced from *North American Range Plants,* 5th edition, by James Stubbendieck, Stephan L. Hatch, and Charles H. Butterfield, by permission of the University of Nebraska Press. Copyright 1981, 1982, 1986, 1992, 1997 by James Stubbendieck and Stephan L. Hatch. Drawings by Bellamy Parks Jansen.

distribution of seeds than the short-range, gravity-based dispersal now produces. If long-distance dispersal was important, once-interconnected plant populations became isolated when the big bison herds were killed, well before the tallgrass prairie was plowed almost out of existence. Exploiting bison as seed dispersers is not usually one of the reasons for preferring them to cattle (Benedict et al. 1995; Licht 1997; Knapp et al. 1999), but it may have been an important one from the point of view of plant community dynamics. Seldom is the connection between bison pelts and plant adaptations for dispersal made today, perhaps because bison are still relatively rare in prairie research areas.

Prairie Dogs. The towns and burrows they build create habitat for many other species (Benedict et al. 1996) making them a keystone species. Many species of mammals, birds, reptiles, invertebrates and plants tend to aggregate on prairie dog towns (Costello 1970; Hoogland 1995). One obvious example is the black-footed ferret (*Mustela nigripes*). As far as is known, black-footed ferrets depended completely on prairie dog towns. By 1972 with the decline of prairie dog numbers, the ferret was believed to be extinct. A remnant population was discovered in 1981. By 1987, this one remaining population was removed from the wild to protect it from extinction by feline distemper. Following a captive breeding program, black-footed ferrets were reintroduced into the wild (into prairie dog towns) in 1991. The black-footed ferret remains the rarest mammal in North America (US Congress 1995; Benedict et al. 1996).

Beyond black-footed ferrets, a whole ecosystem depended on prairie dogs (Costello 1970; Hoogland 1995). The burrowing owl (*Speotyto cunicularia*) provides another example. Although most owls are large, tree-dwelling birds that fly at night and eat mainly rodents (e.g. Johnsgard 1988), burrowing owls are well-adapted to grasslands. Burrowing owls are small (23 cm, 9 inch), live in holes in the ground, eat mainly insects (beetles!) and are active by day (Costello 1979; Johnsgard 1988). In the grasslands of the Great Plains, prairie dog towns provided the most important source of burrows (Desmond and Savidge 1996). Desmond and Savidge (1996) argue that, at least in Nebraska, the numbers of burrowing owls are declining precipitously as prairie dogs decline. Given the data on black-footed ferrets and burrowing owls, it is highly likely that other animals associated with prairie dog towns have been reduced as well (Costello 1970; Hoogland 1995).

Prairie dogs also had complex effects on plant communities. For example, Weltzin et al. (1997) show that prairie dogs limit the abundance of honey mesquite *(Prosopis glandulosa* Torr.), a native shrub whose dramatic increase in numbers is causing a substantial loss of grazing land (e.g., Brown and Archer 1987). Prairie dog activity, and the foraging of ants associated with prairie dog towns, significantly reduced the number of honey mesquite seeds and pods (Archer et al. 1988). Likewise, prairie dogs reduced the survival of seedlings planted into their towns by 60%. Overall, cover and abundance of honey mesquite were much, much lower on occupied prairie dog towns than outside prairie dog towns or in abandoned towns. Thus, Archer et al. (1988) argue prairie dogs are keystone species, and help maintain grassland by preventing the colonization of the southern plains by woodland. However, the status of prairie dogs as a keystone species, although it seems compelling to me, has not been universally accepted (Stapp 1998).

Beaver. These aquatic engineers had disporportionately important effects, playing a keystone role for the rivers. The Great Plains rivers and streams today are braided, often shallow, channels passing between forested banks, except where humans have channelized them. Because of spring floods, summer drought and wildfires, prairie streams were generally thought to have been more open in the past and basically treeless (Shoemaker 1988; Johnson 1994). Few discussions, however, fully integrate our increasing recognition that the beaver lived and worked in the prairie steams and rivers, building dams that created ponds and small forests (Naiman et al. 1988), altering the system for all associated species. By the time Europeans recorded their observations about the rivers, beavers had been hunted back to the Rocky Mountains and their impact on riverine communities was lost (Naiman et al. 1988). As beavers reestablish populations within their historical range, we may be in a better position to reconstruct the dynamics of riverine communities of pre-European times.

Missing species likely had a variety of impacts. One of the hardest to analyze in the absence of the organism is the mess that their activities made and the byproducts of such activity. For example, Knapp et al. (1999) emphasize the consequences of bison carcasses rotting on the prairie, from initial inhibition to subsequent stimulation of plant growth, and also as food for all sorts of scavengers. Generally, one does not notice that modern prairies completely lack decaying carcasses, even though they must have been quite common at one time. Likewise we notice the borrows prairie dogs build, but may not think of the resources provided by prairie dog feces for dung beetles or tunnel entrances as excellent web sites for spiders. Without beavers, wood chips are rare to nonexistent and the submerged tree branch structures do not exist. Presumably such little changes sets up conditions for other species to grow or forage where they previously could not.

Changes in Communities

The impact of grazers on plant communities is clear. Bison eat predominantly grass (Peden et al. 1974; Steuter et al. 1995), and the direct impact on the plant community of the estimated sixty million bison (Roe 1951; Costello 1969) was to reduce the dominance of grasses. Domestic cattle, which likewise prefer grasses in their more diverse diet, can have a similar impact on the grasses where stocking rates are similar (Steuter and Hidinger 1999; but see Benedict et al. 1996; Licht 1997; Knapp et al. 1999). Yet, most tallgrass prairie remnants are ungrazed, and many are regularly burned. Both of these conditions—no bison and use of fire—strongly favor the grasses over other types of plants (Weaver and Rowland 1952; Collins and Wallace 1990; Leach and Givnish 1996). The nearly pure stands of grass often seen in small tallgrass prairie reserves can be seen as a product of our management techniques.

Second, bison and other grazers, after selectively feeding, leave behind local concentrations of nitrogen, as urine and feces. Without grazing, the nitrogen cycle is quite different: the nitrogen in leaves falls as litter and is released by decomposition very slowly (Steinauer and Collins 1995). Nitrogen is an essential element for the growth of all organisms, and it frequently limits plant growth (Seastedt 1995; Smith 1996). Tilman and Wedin (1991) showed that one of the reasons that big bluestem (*Andropagon gerardii*) can become an ecosystem dominant is because it is the most nitrogen-efficient tallgrass species . When nitrogen levels become low, big bluestem is the plant least affected (Tilmen and Wedin 1991). I think it is unlikely that big bluestem was as dominant historically as it is in many prairie remnants today. The disturbance and nitrogen regime of grazed prairies were more favorable for the persistence of other plant species. More important, grazing by bison contributed to limiting big bluestem cover by consuming it, preventing this species from monopolizing key resources, such as nutrients and light.

A medium-to-heavily grazed grassland by cattle can be gradually reduced to only unpalatable grasses and forbs because confined cattle selectively feed on the most palatable species. The prairies Lewis and Clark saw at the beginning of the nineteenth century were inhabited not only by bison but also by elk (*Cervus canadensis*), deer (*Odocoileus virginicus O. hemionus*) and in the west, pronghorn (*Antilocapra americana*) and black-tailed prairie dogs (*Cynomip ludovicianus*) (Benedict et al. 1996; Licht 1997). These herbivores all have diets quite different from bison (Costello 1969; Sexson et al 1980; Singer and Norland 1995). Pronghorns, for example, prefer forbs, leaving the grasses behind (Sexson et al. 1980). Thus, a mix of herbivores should result in diverse stands of plants, not pure stands of grass or pastures of unpalatable plants (Collins et al. 1998; Kaiser 1998). A diverse community of large herbivores, now gone from almost all prairies, promoted plant diversity.

Changes in Other Species

Lost interactions are unlikely to be confined to interactions with keystone species or large mammalian grazers. For example, prairie bird flocks have been greatly reduced and their movement patterns dramatically altered (Batt 1996; Knopf 1996; Licht 1997). Changes in bird abundance and behavior could affect many other species. Changes in birds, of course, will shift the distribution of their invertebrates parasites. Consumption of seeds by birds destroys lots seeds, for example sunflower seeds (Besser 1978), reducing the number that can germinate but dispersing the dropped or surviving seeds. Fewer birds will result in more seeds available to germinate but fewer scattered seeds. Additionally, birds disperse some seeds without eating them, for example, the grassland varieties of cherries (*Prunus pumila* var *besseyi*), grapes (*Vitus acerifolia* Raf. and*V. vulpina* L.) and poison ivy (*Toxicodendron radicans* [L.] O. Ktze.). When birds are forced to concentrate in an area because of reduced habitat (e.g., Batt 1996), seed dispersal patterns will reflect those changes. Bird consumption of seeds could be critical to the numbers of inconspicuous plants, e.g., small grasses or species such as the euphorb *Croton texensis* (see Cook et al. 1971).

Invertebrate species and mammals are likely to have changed too. For example, recent studies indicate that the number of butterflies have decreased on many prairie remnants (Debinski and Kelly 1998; Schlicht and Orwig 1998). One plant thought to be negatively affected by changes in the insects is *Ruellia humilis* Nutt. (Acanthaceae). Although the attractive blue-purple flowers suggest that a moth or butterfly typically transferred pollen between plants, J. C. Heywood (personal communication) has shown that in Missouri prairie remnants the plants have little genetic variation and are very much like their neighbors, apparently because the flowers almost exclusively self-pollinate. Presumably the insect that originally transferred pollen between *Ruellia* is extinct from small Missouri prairies. In fact, loss of pollinating insects may be a more common phenomenon than generally appreciated (Buchmann et al. 1996; Kearns et al. 1999).

The impact of species losses in prairie remnants may not be readily apparent. For example, it can be difficult to discover whether wildflower populations are declining. Individual prairie plants have lifespans ranging from a year to centuries (e.g., Keeler 1987, 1991; Hartnett and Keeler 1995; Weller et al. 2000). Poor recruitment of new plants may not be noticed if the large, old individuals flower conspicuously. By the time older plants senesce and declines in flower abundance are obvious, the populations may be drastically reduced. Menges and Dolan (1998) following up earlier work (Menges 1991) of the now rare prairie wildflower, the royal catchfly (*Silene regia* Sims, Caryophyllaceae), have found that small populations had significantly poorer seed set than did large populations, presumably because they crossed only with close relatives and so produced largely infertile seeds. As a consequence, the royal catchfly in some prairies is present and flowers well, but rarely reproduces.

To document changes in prairie plant communities, Leach and Givnish (1996) revisited prairies in Wisconsin that were described before 1960. They found that the prairies they studied had lost 32-52% of the plant species present in the first survey. The plant species lost tended to be small in stature and to grow in the moist parts of the prairies. An attractive stand of tallgrass prairie today may, in fact, have many fewer species than a similar area two hundred years ago. Where there are missing species, an ecologist suspects that there are missing interactions, interactions that influence the success of the surviving species.

Past Climates

Finally, there is evidence that climate changes also have changed prairie interactions. In Europe the major mountain ranges run east-west. Consequently, Pleistocene glaciations caused the extinction of plants that were trapped by the mountains preventing their southward migration as temperatures declined (Pielou 1991). In the Americas, however, the large mountain ranges tend to run north-south. Plants were able to migrate southward as the glaciers grew, and the level of extinction was much lower (Pielou 1991). Presumably, without mountains barring northward migration and more than 8,000 years since the last glaciation, American plants should have reached as far north as their ecological tolerances can take them, especially in the Great Plains. However, Brown and Gersmehl (1985) argued that the patterns of grass distribution suggest that several species, such as big bluestem and blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths), have not yet reached as far north as their physiological limits. What other species—forbs, invertebrates—might still be south of their climatic limits because of slow migration rates? James (1991) suggested that differences between the earthworm communities of the northern and southern Great Plains might be better ascribed to history than to present climate. He found many more earthworm species in unglaciated than glaciated regions.

More recent effects of climate on the distribution patterns of organisms are also probable. The Great Drought of the 1930s caused displacement of species (Weaver and Albertson 1936). For example, in Nebraska tallgrasses died off on the tops of hills and they were replaced by mid and short grasses (Weaver and Albertson 1936), only to return when conditions improved (Weaver and Albertson 1943). While large prairie remnants would have had seed sources for recolonization, smaller prairies might not have. Tilman and El Haddi (1991) reported that in 1988 drought reduced the number of species at a Minnesota prairie site by 37%. After two normal growing seasons, only 5% of the lost species had reappeared. The authors suggest that lack of seed sources generally limit recolonization after drought, even on this very local scale.

Conclusion

There is evidence that many changes have occurred in North American prairies since the glaciers last retreated. Some species have been added, others were lost. We can study the interactions with added species directly, but it is easy to overlook the effects of the missing species. Yet, things as obvious as pronghorn speed or plant distribution may have been a consequence of interactions with the now-missing species. To interpret these things accurately, we must consider the influence of interactions with species that are no longer present.

I believe that the factors that structured prairies are knowable even if some species have vanished. In fact, I view it as an exciting challenge. Considering the impact of missing interactions should help us better understand what we see today. To test ideas about the role of missing interactions, studies can be done in remaining relatively intact systems. These include several large preserves of tallgrass prairie in Kansas and Oklahoma, as well as the grasslands in the Nebraska sandhills and the high plains that are used for cattle production. In addition, the grasslands of Yellowstone National Park, the North American system with an apparently complete fauna including big native predators, provide an important opportunity for such research.

All ecosystems on earth change with the climate and in response to extinctions. The same is true for the Great Plains. Here, however, we have little historical or geological record upon which to draw to understand what interactions might be missing. If we are alert to the possibility of lost interactions, we are likely to be able to better explain the interactions we see.

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